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THE ORIGIN AND RELATIONSHIPS OF THE ARAUCARIANS. II

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The abietinean theory

This theory has developed more or less gradually and can best be understood by tracing the historical sequence of discovery and the ideas of relationship that have grown out of them.

1. Foremost in time and importance was the discovery that the steles of ferns, gymnosperms, and angiosperms are characterized by a leaf gap opposite the departing leaf trace. To this group was given the name Pteropsida. To the remaining groups of vascular plants the name Lycopsida was applied. This conception grew out of the investigations of the anatomy of *Equisetum* (27), the stem of angiosperms (28), and the structure and development of the stem in pteridophytes and gymnosperms (29). This distinction between these two great groups has been widely accepted by botanists and has formed one of the most fundamental objections in the minds of many (16, 53) to the lycopod theory. It has been questioned by the adherents of the latter theory (54, 61), but only in so far as to deny that a phyllosiphonic siphonostele (Araucarineae and possibly other conifers) might have arisen from a lycopod ancestry. The contention is that this type of stele is merely one of the important milestones along the evolutionary highway along which all vascular plants tend to travel. It is conceived to be in the same category as the heterosporic habit, the seed habit, and the tendency to reduce the size of the gametophytes.

It still remains true, notwithstanding that no known lycopod did actually cross the line.

2. Two years later (1904) came the statement of certain canons of evidence, some of which were well known and had already been employed by zoologists and to a certain extent by botanists. These are stated by JEFFREY (31) as follows: (1) ancestral characters that have disappeared from the vegetative axes are apt to linger in (*a*) reproductive axes, (*b*) foliar organs, (*c*) seedlings (ontogenetic recapitulation of the zoologists), (*d*) first annual ring of vigorous shoots; (2) ancestral characters may be recalled by wounding.

These canons of evidence have been consistently applied and somewhat extended in all of the subsequent work. They have been used to check conclusions derived from comparative anatomy (resemblance) and geological sequence, and in some cases practically overrule them. A really astonishing number of forms, both fossil and living, has been studied by JEFFREY and his associates in the last dozen years. Although not always without serious protest, they have been able to interpret all these forms in conformity with the general assumption that the Araucarineae have been derived from an abietineous ancestry. Much of the most important material has come from the Mesozoic of eastern North America.

A complete review of all this work is neither necessary nor profitable. Essentially the same methods have been employed in all of it. Reference will be made only to those papers in which important new facts or an advance of ideas are contained.

3. It must always be borne in mind that this school of anatomists is firmly committed to the brachyblast theory of the pine cone (19, 42, 58). From the vantage point of this conviction they extend the conception to the ovulate cones of all other conifers, and regard the spur shoot of the pines as the homologue of the assumed axillary sporangium-bearing shoot of the cones. The contention is that the spur shoot has disappeared from most modern conifers, as represented in its most primitive form in such ancient conifers as *Prepinus* and *Woodworthia*.

4. An additional canon was provided (1910) by Miss GERRY'S study of the distribution of the bars of Sanio in living conifers (20). She concluded that this structure is present in the mature secondary

wood of all conifers except the Araucarineae. It has since been used by this school as the *sine qua non* in distinguishing fossil araucarian woods from those of abietinean affinities (9, 24, 25, 57).

An early application (1906) of these principles was made by JEFFREY and HOLLICK (32). Certain of the remains studied consisted of cone scales that had previously been referred to plants of such diverse relationships as *Dammara*, fossil genera belonging to Cupressineae and Taxodineae, and even to *Eucalyptus*. These scales have three basally attached and inverted seeds on their adaxial surface. There are longitudinal resinous lines on their surface. The internal structure, particularly the arrangement of the vascular supply, is very like that of *Agathis*. For these reasons they have called the plant *Protodammara*.

Closely associated with the scales were branches of *Brachyphyllum*. The authors think it probable that the branches and cone scales belong to the same plant. The branches were sectioned and referred to the Araucarineae on the ground that of the three groups (Cupressineae, Sequoiineae, and Araucarineae) which they externally resemble, only the last agrees with them in the possession of a double leaf trace, insoluble resins accompanied by mucilage, and flattened bordered pits which may rarely be alternate and biseriate. Moreover, these branches lack the alternating bands of hard bast in the phloem characteristic of all the living members of the first two groups.

The wood fragments were of two kinds. One of them agrees with the *Brachyphyllum* branches in lacking resinous tracheids and in forming traumatic resin canals. This wood is believed by the authors to be the wood of *Brachyphyllum*. The other wood has resin tracheids and does not form traumatic resin canals. The inference from these facts is that araucarians, as represented by *Brachyphyllum*, have come from ancestors with resin canals.

In the same year (1906) JEFFREY and CHRYSLER (33) described certain cretaceous Pityoxyla from the same source as the *Brachyphyllum*. These Pityoxyla appear very probably to be the wood of cretaceous pines, since they are very closely associated with typical cone scales and leaf fascicles of this genus. These pines appear to have combined the characters of hard and soft pines.

The scales and leaves resemble those of the hard pines, while the presence of abundant tangential pitting of the autumn wood is a character of soft pines. The ray cells are highly resinous, and there are no ray tracheids such as are characteristic of the Pineae. The authors point out that these are just the characters shown by the wood of the cones of hard pines. They enforce their argument from vestigial structures in the following words: "there can be little doubt that in the wood of the cones of *Pinus palustris*, for example, the general absence of marginal tracheids, the highly resinous character of the rays, and the abundant presence of tangential autumnal pits, all features of difference from the vegetative wood structure of existing hard pines, are ancestral characters, since such characters are apt to linger on in the reproductive axes. In no other way can the presence of these features in the wood of the cone be explained." They call attention to the great geological age of the pines as further support of the application of these principles. "There is good reason to believe from recent researches (33) that the genus *Pinus* in essentially its modern form, so far as the external features of the female cones go, existed as far back as the Jurassic. There is even evidence that the two great series of the hard and soft pines existed at this early period, so that the geological extension of the genus must have been much more remote."

Following up the same line of reasoning, JEFFREY (34), in a paper on wound reactions of *Brachyphyllum*, put forward the suggestion that "there is nothing inherently improbable in the derivation of the Araucarineae from an abietineous stock." He puts forward three sorts of evidence in support of this suggestion.

In the first place, he points out, the wound reactions of *Brachyphyllum* are of exactly the same character as those of *Sequoia*. In a previous investigation he was led to conclude, from the traumatic production of resin canals, taken in conjunction with their vestigial occurrence in the cone axis, first annual ring of the stem, and in the root, that resin canals were characteristic of the ancestors of *Sequoia* (30) as well as of *Abies* and certain other Abietineae (31). By combining the vestigial structures exhibited by the cones of the living araucarians with the wound reactions of *Brachyphyllum*, he is led to infer a similar ancestry for Araucarineae.

The second proof brought forward in support of this conclusion is that the triassic *Araucarites moniliforme* (34) is reported to have strings of flattened moniliform masses of resin in the wood. The author thinks that such masses of resin would be produced by resin canals larger than those of *Brachyphyllum*. Apparently there is a reduction series in resin production in the Araucarineae. It is abundantly secreted in the canals of the triassic *Araucarites*, less abundantly in those of the cretaceous *Brachyphyllum* and only when wounded, and resin canals are entirely absent in living genera.

As a third proof a still stronger claim is made again for the antiquity of the pines. The author points to the recognized impressions of pine leaves from the Permian onward, of hard and soft pines after the Jurassic, and of Pityoxyla from the Carboniferous and Permian. It should be recalled that both the Permian and Carboniferous Pityoxyla have since been rendered extremely doubtful by the work of GOTHAN (21, 22) and of THOMSON and ALLIN (71), though undoubted Pityoxyla are known from the late Jurassic onward.

Araucariopitys was described (35) in 1907. The description is based on certain leafless twigs with spirally arranged scars. They were found in the Androvette pit (Cretaceous) in association with "impressions of the deciduous leaf fascicles of *Czekanowskia*, a supposed but doubtful representative of the Ginkgoales." It is inferred, with some hesitation, that the two belong to the same plant. It is shown that *Araucariopitys* had deciduous spur shoots lasting, very probably, only a single year. Traumatic resin canals were produced; the ray cells are pitted on sides and ends; the pits are usually uniseriate, round, and remote, but may occasionally be biseriate and alternate or opposite, in which case they are sometimes flattened. The uniseriate pits are also sometimes flattened and in contact. It is rather difficult to credit close araucarian affinities to this plant when one considers that it resembles a *Ginkgo* externally and has the spur shoot and pitted rays of the pines, as opposed to the slight resemblance to araucarians in the occasional occurrence of alternate and flattened pits. The authors, however, decide in favor of its being an araucarian on the ground of its close association with other araucarian woods and transitional cone scales. If this plant really is, as the authors think, an abietinean in process of transformation, it would appear to be a question whether it were headed toward *Ginkgo*, which it resembles in external features, or toward an araucarian, which it does not resemble externally and toward which it has made but a very small beginning structurally.

In 1908 *Prepinus* was described (37). The name was proposed "for this type in the belief that it is the direct ancestor of *Pinus*." "It is characterized by the possession of short shoots or brachyblasts of a generalized type, which were deciduous, but bore numerous spirally arranged instead of few verticillate fascicular leaves." "The leaves attached to the brachyblasts differed from the fascicular leaves of *Pinus* in having their paired resin canals continuous to the very base. The leaves further possessed well marked centripetal xylem. About the foliar bundles was present a complicated double sheath of transfusion tissue closely related to the centrifugal wood and resembling that found in certain of the Cordaitales." "Many of the true pines of the Cretaceous possessed the same double transfusion sheath as is found in *Prepinus*, but entirely lacked the centripetal wood which is characteristic of that genus." "The elongated pitted elements described by WORSDELL and others on the ventral side of the protoxylem in existing coniferous leaves appear rather to be the relics of the inner transfusion sheath, which is a feature of cretaceous pines, than of true centripetal xylem."

From the resemblance of the leaf structure to certain Cordaitales, the conclusion is reached that the Abietineae are "a very old, if not the oldest, family of the Coniferales." From this argument, and others already detailed, it is concluded that "the Abietineae must be considered more primitive than the Araucarineae." What at first sight appears to be a new argument in support of this contention is introduced in this paper. "The pitting of the older Araucarineae, which still survived in the Middle Cretaceous, showed a marked deviation from that found in *Agathis* and *Araucaria*, and a transition toward the type of pitting found in the Abietineae, while the oldest structurally known type of the Abietineae (*Prepinus*) shows no tendency whatever toward the araucarian type of bordered pits." There is, however, nothing new in this statement, for its entire force depends upon whether these intermediate forms are called araucarians or not. It is, of course, precisely the point at issue whether these intermediate forms are of araucarian descent on the way toward becoming Abietineae or the reverse. In fact, if this statement could be substantiated, it would completely overthrow the abietinean theory of the descent of araucarians, for this theory demands that Abietineans shall have departed in many characters, not only toward araucarians, but that this departure shall have continued until the latter were actually reached.

In 1909 SINNOTT (57) described from Second Cliff, Massachusetts, another fossil conifer, which he referred to a new genus, *Paracedroxylon*. The pits are uniseriate, remote, and round. The rays are without marginal tracheids, and the cells are thin-walled and without pits on the ends or horizontal walls. Simple pits occur on the radial walls corresponding to the half-bordered pits of the adjacent tracheids. Resin canals are normally absent, and no sure evidences were found of their traumatic production. The new genus, nevertheless, is assigned to the Araucarineae on the ground that bars of Sanio are absent. As I shall point out later, other anatomists have strongly objected to the reference of fossil woods to the Araucarineae on this ground.

In 1911 JEFFREY described the structure of the cone of *Geinitzia gracillima* (41) from the Kreischerville beds. This piece of investigation furnishes a very interesting application of the canons of evidence that have been applied in the attempt to seriate these fossil types, for it furnishes an attempt to make a comparative study of the structures of the vegetative and reproductive axes of the same fossil plant, and to apply to the results the canon of vestigial structures. The external appearance of the cones, as well as the individual scales, are very reminiscent of certain Taxodineae. The branches are thought to be *Brachyphyllum*. The structure of the cone axis is that of SINNOTT'S *Paracedroxylon* (57). From these facts the conclusions follow that *Paracedroxylon* is ancestral to *Brachyoxylon;* that the evolutionary sequence must have been Abietineae (*Pityoxylon*, perhaps), *Paracedroxylon*, *Brachyoxylon*, *Araucarioxylon*, modern Araucarineae. It will be pointed out later that this scarcely accords with the strict geological sequence as known at the present writing.

Woodworthia arizonica was described in 1910 by JEFFREY as a new genus from the triassic petrified forests of Arizona (38). It agrees in all respects with *Araucarioxylon*, with the exception of possessing short shoots and the absence of persistent leaf traces. The spur shoots are thought to persist as long as the axis which bore them. The spur shoots are held to show a relationship to the pine type of conifer. The failure of the subtending leaf traces to persist indefinitely, as in living forms, is held to be an argument against this persistence being a primitive character. Notwithstanding the fact that the cretaceous *Araucariopitys* is much more abietinean in all respects and a much more modern type, the author is still disposed to cite the two as evidence of "the tendency of the Araucarineae to become more and more like the Abietineae."

In 1911 BAILEY described a cretaceous *Pityoxylon* with marginal tracheids and concluded (2) that such marginal tracheids originated in the Upper Cretaceous. In a paper published in 1913, Miss HOLDEN has extended our knowledge of the generic and geologic distribution of ray tracheids (25). She concludes from her study that (1) "ray tracheids are present normally in the Pityoxyla from the Middle Cretaceous on, and in the Abietineae"; (2) "ray tracheids are present traumatically in the Taxodineae and the Cupressineae"; (3) "on the evidence of traumatic recapitulations of ancestral characteristics, it is evident that the Taxodineae and Cupressineae are descended from the Abietineae, having sprung from that line sometime after the Middle Cretaceous"; (4) "since ray tracheids are universally absent in the Podocarpineae, Taxineae, and Araucarineae, these lines must have come off the Abietineae at some time before the Middle Cretaceous."

In 1912 JEFFREY published a very complete résumé (42) of his views and investigations. The first part of the paper deals with wood parenchyma and medullary rays. He concludes: (1) "The ancestors of *Araucaria* and *Agathis* were characterized by the possession of wood parenchyma." This conclusion rests on the facts that, though the living forms resemble the Cordaitales in the absence of wood parenchyma, it is present in the first annual rings of the root and shoot of both *Agathis* and *Araucaria*, in the early wood of seedlings, in the wood of the cones, and may be traumatically recalled in the older wood of both root and shoot. Furthermore, it is present in the more abietinean Araucarioxyla of the Cretaceous. (2) "They likewise had strongly pitted rays." This is shown by their presence in the inner portion of the cone axis of living forms and in the normal wood of those cretaceous forms (*Araucariopitys*, for example) which the author assigns to the Araucarineae. Pitted rays may also be recalled in the seedling and root by injury. (3) "The possession of these two features is quite inconsistent with their derivation from cordaitean ancestry," notwithstanding the practical identity of structure of the two groups. This argument rests partly on recapitulationary phenomena and partly on merely calling the transitional cretaceous conifers araucarians rather than abietineans, which some of them resemble far more closely.

The second part deals with "the characteristic features of the tracheids and the nature of the pitting." The conclusions are: (1) "The characteristic pitting of the wood of *Agathis* and *Araucaria*, the *Araucarioxylon* type, is not ancestral but more recently acquired." This conclusion is based on the fact that the multiseriate, flattened, and appressed pits of the mature wood of living araucarians and of Cordaitales is replaced in the inner wood of the cone and seedling axis of living genera and in the innermost wood of the stem of mesozoic forms by a type of pitting with the pits less frequently multiseriate, flattened, or appressed, but often uniseriate, remote, and round. (2) Since bars of Sanio are absent from the mature wood of living genera (see THOMSON 70 for a contrary opinion) and from the wood of mesozoic Araucarioxyla, but are present in the wood of the cones, it follows that they are a feature of the ancestors of the Araucarineae. In anticipation of objections to be urged later, it may be mentioned here that the author admits their absence in the stem of the mesozoic forms, in the seedling, and probably in the leaf trace, in all of which they should be found in accordance with theoretical expectations. (3) "On the basis of comparative studies of the tracheids of the Araucarineae they cannot be regarded as primitive representatives of the coniferous order."

The third part deals with resin canals. Two reasons are alleged for thinking them to be features of the ancestors of araucarians: (1) Though they are practically absent from living araucarians, "interesting vestigial resin canals appear in the vascular supply of the lowermost abortive cone scales, attached to the peduncle of the cone, and die out before the cone scale supply leaves the wood of the peduncular axis." (2) Traumatic resin canals occur in the wood of some mesozoic woods which the author assigns to the Araucarineae because of the lack of the bars of Sanio and the possession of a modified type of pitting. The pitting in the *Araucariopitys* type, as has already been pointed out, is very little like that of araucarians and very much like that of abietineans, as are, in fact, its other characters. The *Brachyoxylon* type is rather more reminiscent of araucarian affinities but still not beyond challenge.

The fourth part treats of the foliar trace and the pith, and presents a final summing up of conclusions. In regard to the leaf traces and pith the conclusions are: (1) "This persistence of the leaf trace [that is, in mesozoic forms] seems to be a characteristic of all woods of the true *Araucarioxylon* type, and, as has been particularly indicated by THISTLETON-DYER (**66**) and SEWARD (**54**), is likewise a feature of the trunks of the living genera *Agathis* and *Araucaria*." (2) In the *Brachyoxylon* type from the Cretaceous, which is more abietinean in the rays, pitting, and in the formation of traumatic resin canals, the traces persist for a short time only. (3) In the seedling axis of *Agathis australis* the leaf trace is less persistent. (4) The leaf trace is more persistent in *Araucaria Bidwillii* than in *Agathis australis*, the former of which is assumed to be the more primitive type. (5) It follows from the preceding that persistent leaf traces are not an ancestral feature of the Araucarineae. (6) In regard to the pith I am not at all sure that I apprehend clearly JEFFREY'S position. He records the usual presence of sclerotic diaphragms in the pith of mesozoic forms, and finds them absent in the pith of the seedlings and cones of living forms. Sclerotic nests are said to occur in the latter, perhaps as a vestige of the diaphragms of the earlier forms. He says further that "it is moreover obvious that medullary diaphragms are equally characteristic of both the older Araucarineae and of the Abietineae living and fossil. Their presence in the older araucarian types, consequently, is one more piece of evidence in favor of the derivation of the araucarian tribe from abietineous ancestors." (7) The author reiterates his belief in the compound nature of the ovulate cone and in its essential unity throughout the group. He says, "it is perfectly clear that not only in the more primitive species of the living genus *Araucaria*, but also in the cones of the mesozoic representatives, the araucarian female cone, like that of the other tribes of conifers, was originally composed of cone scales with a double system of bundles, independently emanating from the cone axis and of inverse orientation." (8) In regard to the male gametophyte he says, "certainly we should not expect to find the primitive type of pollen tube formation in a group in which the pollen no longer reaches the apex of the ovule," and "the peculiar method of germination of the pollen is an unmistakable stigma of aberration." "The contents of the pollen tube likewise vouch for the highly specialized condition of the Araucarineae. Here the two prothallial cells common to the Abietineae and the equally ancient Ginkgoales become proliferated into a large number, doubtless in correlation with the extreme length and meandering course of the pollen tube. Moreover, the absence of a stalk cell in connection with the setting off of the body cell, which gives rise to the two sperm cells, is a clear and outstanding feature of aberrancy." These views are in a measure a modified restatement of those stated by JEFFREY and CHRYSLER in 1907 (36). JEFFREY is equally convinced that the female gametophyte is not primitive but aberrant.

In a very complete study of *Agathis* (19) EAMES has reached conclusions closely paralleling those of JEFFREY in regard to the specialization of the gametophytes and the interpretation of the structure of the ovulate cone of the araucarians. An interesting and important feature of this investigation is the very complete reduction series which he has worked out in the supposed development of the apparently simple scales of *Agathis*. Beginning with *Arthrotaxis cupressoides* with a completely double vascular supply, he traces the gradual fusion of the independent bundles through other species of the same genus, *Cunninghamia sinensis*, and finally reaches the condition found in *Agathis*. He also points out that a complete series is exhibited in the genus *Araucaria* with *A. Bidwillii* standing as the most primitive and *A. brasiliensis* and *A. imbricata* as the most specialized. In preceding papers of this series the reviewer has discussed EAMES'S views in relation to the gametophytes (6) and the embryo (7).

Although SINNOTT (59) concludes from his study of the podocarps that they have been derived from the Abietineae directly, and not through the Araucarineae, his view is incidentally interesting in that it points out that on this assumption the podocarps become the primitive members of the group instead of the *Saxegothaea-Microcachrys* forms. In his diagram it would appear that he thinks this whole assemblage derived from the ancient Araucarineae, and that they had arisen by an approximately equal split of some ancient Abietineae, the other arm being the modern abietineans. From the text, however, it appears that "the close series of forms from *Podocarpus* to *Saxegothaea* is very suggestive as offering a key to the evolutionary development of the modern Araucarineae." The argument turns on the interpretation of the vascular supply in these forms as a reduction series and the epimatium as the equivalent of a reduced ovuliferous scale. He calls attention to the already well known gametophytic resemblances, which his own studies have rendered more apparent, as evidence of a relationship between podocarps and Abietineae. In like manner he minimizes the points of difference. He recognizes that his series can be read in the other direction, and calls attention to the necessity in that case of recognizing and accounting for what would be numerous parallel developments in the two lines.

In the concluding section of his paper on the *Araucarioxylon* type (42) JEFFREY sums up the conclusions for the whole theory as follows: (1) "The Araucarineae cannot have been derived from the Cordaitales since they possessed primitively a number of features which, so far as our knowledge goes, never existed in the cordaitean stock." (2) "The *Araucarioxylon* type is derived from ancestral forms which possessed opposite pitting, bars of Sanio, strongly pitted rays, and horizontal and vertical resin canals." (3) "The primitive existence of these features in the ancestral type from which *Araucarioxylon* has been derived shows clearly that it has taken its origin from the abietineous *Pityoxylon* type." (4) "This conclusion is entirely confirmed by a consideration of the reproductive structures, both sporophytic and gametophytic." (5) "Any hypothesis as to the origin of the Coniferales in general must start with the Abietineae as the most primitive tribe."

This theory has received from time to time certain incidental criticism in connection with the work of investigators who have considered that their results justify other interpretations. A number of these have already been mentioned in the presentation of the lycopod and cordaitean theory. It is in the nature of things that the facts which form the support of one theory are usually the facts that refuse to adjust themselves easily to others. Objections of this sort have found their proper place in the preceding paragraphs. I shall now mention some of the more specific objections that have been made.

It has already been pointed out that the protagonists of the lycopod theory hold the ovulate cone of the araucarians to be simple. The abietinean theory is circumscribed by the necessity of proving it compound. The weight of opinion, at least so far as numbers go, among those who have investigated the subject appears very decidedly to favor the idea that the ovulate structures of podocarps and araucarians are homologous in structure and simple. It appears from the work of EAMES and SINNOTT, already quoted above, that if the abietinean theory prevails they can be explained as a reduction series. On the other hand, if this theory were not in question, it appears that most investigators would decide in favor of simplicity of structure. Aside from the authors already mentioned, TISON (76) and NOREN (44) have expressed themselves in favor of a simple explanation.

The writer has in earlier papers called attention to the inadequacy of the explanation offered by JEFFREY and CHRYSLER (36) of the more numerous prothallial cells in the gametophytes of podocarps and araucarians. These authors suggested that the greater number of these cells might be a coenogenetic adaptation to the extensive pollen tube. Aside from the reasons for thinking that the tube itself has not undergone any such coenogenetic development as this theory suggests (by implication) for the araucarians, it is entirely inapplicable to the podocarps and *Abies* (26), which has recently been shown to form regularly a considerable proportion of pollen grains with 3 or 4 prothallial cells. Either these widely separated cases are to be explained as a heritage from more or less remote ancestors, or as remarkable examples of the revival of abandoned structures, or as the still more remarkable origination of apparently useless structures. In JEFFREY'S paper on the *Araucarioxylon* type (42) he speaks of the pollen grain and male gametophyte as clearly aberrant in its germination, prothallial cells, and absence of a stalk cell. Whether it is aberrant or not is doubtless somewhat a matter of opinion. That a stalk cell is not formed is an error so far as the statement concerns *Araucaria brasiliensis*. I have figured in a previous paper the division which results in stalk and body cells (5). *Araucaria* resembles *Podocarpus* (4) exactly in respect to the manner of this division. The axis of the spindle is transverse in both cases and the resulting cells lie side by side above the prothallial cells. Because this division occurs late in the development of the male gametophyte, the cell wall and cell identity of the stalk cell are soon lost in both genera. At the time of shedding, only the body cell retains its cell identity, the other nuclei being free in the common cytoplasm and often indistinguishable from one another.

The reference of some of the mesozoic fossils to Araucarineae has met with rather severe criticism. JEFFREY'S reference (40) of *Yezonia* and *Cryptomeriopsis* (62) to *Brachyphyllum* and *Geinitzia* respectively has met with opposition from their authors (63). Dr. STOPES, notwithstanding the dissimilarity of the cones, is inclined to agree that there is a considerable structural resemblance between *Brachyphyllum* and *Yezonia*. She dissents entirely from the opinion that *Cryptomeriopsis* is an araucarian. She has not stated an opinion as to whether it is or is not identical with *Geinitzia* as described by JEFFREY (41). She is emphatic, however, in thinking that it differs very little from the modern *Cryptomeria*.

STILES (61) has also criticized the reference of *Geinitzia* (41) and *Paracedroxylon* (57) to the Araucarineae. He is particularly severe on the use of the bars of Sanio as a final criterion of relationship. The soundness of this criticism has since been emphasized by

THOMSON'S discovery of these bars of Sanio in the ordinary wood of araucarians (70). They have also recently been reported in the cycads (56). In this group they are said to occur when the pits are scattered, but not when alternate and crowded.

THOMSON (70) has suggested that the araucarian affinities of some of the mesozoic transitional forms with traumatic resin canals would be equally well explained as having descended from the cordaiteans as by the assumption that they are acquiring araucarian characters. If I understand this suggestion correctly, it assumes that these forms are not directly related to araucarians at all, but are really abietineans that still retain some cordaitean characters and have acquired or are in the process of acquiring the characters of modern abietineans.

On the principles of evidence

After having set forth the evidence that has been adduced by various writers in support of the several theories, it is now pertinent to return to the problem originally proposed by the quotation from JEFFREY. Are there any general principles of evidence or are there not? Are all sorts of evidence of equal value? Shall any class of evidence be excluded, as is done in our law courts? Such questions as these must be answered by every botanist before he can properly proceed to sound inferences from the facts uncovered by his investigation. The arguments set forth in the preceding sections may be conveniently grouped under the following heads: (1) resemblance or likeness, (2) geological sequence, (3) vestigial structures, (4) ontogenetic recapitulations, (5) traumatic reversions, (6) abnormalities or monstrosities.

1. *Resemblance or likeness means relationship.*—This appears to be the most fundamental principle in the minds of the great majority of writers on this and other phylogenetic problems. That this is a sound principle is unquestioned. No fact in our biological experience is better grounded than that "like begets like." That the parent and child may differ in minor points is an everyday experience, but that they ever differ by large differences is not believed. The theory of evolution itself is founded firmly on these two well known facts of general likeness with slight variations.

From this it follows that affinity is roughly proportional to resemblance. Resemblance in one or a few points may mean a slight degree of affinity, or it may merely show a case of parallel development. Heterospory and the seed habit are excellent illustrations of the latter. If, on the contrary, two plants are very similar in all of their organs, the resemblance is usually considered unimpeachable evidence of close affinity. The classification of all our living plants is almost exclusively based on this principle.

A corollary of this principle is that neither of two supposedly related plants must possess any organ or structure which cannot be reasonably derived from the homologous organ or structure of the assumed ancestor.

2. *The geological sequence* should roughly conform to the proposed evolutionary sequence in the development of a modern group from an ancient one. It is obvious that if all the intermediate forms have been fossilized and all discovered, this agreement would be exact and complete. Such conditions doubtless never occur. Since evolution of related forms cannot be supposed to run exactly parallel in different lines, it follows that the discovered fossils from any given horizon might be expected to show one structure or organ ahead in one and another in another. An important corollary of this has frequently been insisted on by COULTER (14, 15, 16). One line of plants may run ahead along a certain line and remain practically stationary for ages in some other. For these reasons and because the fossil record is always very incomplete, inferences from geological sequence must always be subject to considerable doubt.

3. *Vestigial structures.*—By this is meant that anatomical characters that once were general through the entire plant are likely to be retained in certain supposedly primitive regions of the plant, such as the root, cotyledons, cone axes, and leaves. The use of this principle is attended with very considerable difficulties and may frequently lead to very erroneous conclusions. The difficulties lie in two assumptions that must be made in its application. First, we must assume that the stem structure of a paleozoic (let us say) plant was also present in the cone axis. Then when we find this same structure in the cone axis of a modern plant, we must again assume

that this structure is a retained one and not a newly acquired one. If we could avoid the first assumption (that is, if we knew the structure of the ancient cone), we should not need this principle, but could apply the principle of resemblance. Neither is it always easy to decide the correctness of the second assumption. Its limitations, therefore, are clear. It is useful in enabling us to infer a likeness which we do not know actually to have existed. It is, consequently, of much lower value than a direct comparison of known structures. Its highest possible value would equal that of a direct comparison between the homologous parts of the two plants, while its lowest value is actually zero.

4. *Ontogenetic recapitulations.*—This principle assumes that there will be formed in the juvenile stages of a plant or animal organs or structures that were characteristic of the adult ancestral forms. In the form I have stated it, this principle is almost certainly invalid. This is the form in which it is commonly applied. What is probably true is that related animals and plants resemble one another and their common ancestor at all stages from the egg to the adult, inclusive, in all those organs and structures which have neither been lost since the separation from the parent stock nor added to either of the descendants. This principle is not infrequently applied in such a manner as to deprive the conclusions of any real validity whatever. In so far as it possesses validity at all, it owes it to a direct comparison of homologous structures in the same stage of development.

5. *Traumatic reactions.*—When a plant or animal is wounded it not infrequently reacts by forming organs or structures that differ from those usually formed. In some cases these structures are such as are thought to be identical with those of its ancestors. There is no a priori reason why they should be reversions, so far as I can see, unless the original structures were introduced into the sum of the hereditary qualities through wounding in the first place. Pruning a grape vine or a fruit tree usually induces a yield of larger fruit or even a greater total quantity. Increased physiological activity is a very common result of wounding, but it does not therefore follow that this is an ancestral quality of the stock. Some of these responses may represent ancestral conditions, but it seems to

me to be very unsafe to infer that any particular one is so, without independent proof thereof.

6. *Monstrosities or abnormalities.*—So far as concerns inherited abnormalities, it must be true that in the long run the progressive changes must have much exceeded the reversions, else evolution from the simpler ancestors to the more complex descendants of today could not have occurred. This argument cannot be applied in the same way to non-heritable abnormalities, though there is no obvious reason why they should follow any different law of probability. By themselves, abnormalities afford evidence of little weight, since it is impossible to say whether they represent reversions or other chance variations.

Conclusions

We may now attempt to apply these criteria of evidence to the arguments that have been offered by the various supporters of each of the theories. So far as concerns the lycopod theory and the cordaitean theory, it is readily seen that each of them is founded on certain more or less striking resemblances. The evidence, then, is valid so far as the principles are concerned. The weakness of each theory lies in the necessity of certain more or less plausible explanations that must be accepted before the resemblances are evident. The lycopod theory must explain away the very apparent difference in the stelar structures of the two groups and must show how the pine cone has been evolved from the simple cone of a club moss. Without repeating what has already been set forth in other parts of this paper, let it suffice to recall the very large number of points of difference that must be explained away and the comparatively few points of likeness relied on to establish a relationship.

On the contrary, the points of resemblance between araucarians and Cordaitales are numerous and striking. The points of difference are few, and for the most part more easily explained away than those that confront the preceding theory. The geological record appears also to favor the cordaitean theory, for none of the fossil forms are known to approach lycopods in any character more closely than do the modern forms. In fact, it would appear from our present knowledge that the fossil forms were less like them than the modern ones. This would strongly indicate parallel development of similar structures in the two groups. On the evidence, then, as it stands, we must decide that the cordaitean theory is much the more probable.

In respect to the abietinean theory we meet a different state of affairs. It is not claimed that Abietineae are more like cordaiteans than araucarians, but that it can be shown that the likenesses of the latter have been secondarily acquired. This is not parallel development. The theory assumes that a considerable number of characters underwent extensive modification during the evolution of the primitive conifers (that is, abietineans). Multiseriate bordered pits of the cordaiteans became uniseriate, remote, and rounded. The thin-walled unpitted ray cells became thick-walled and pitted. Resin canals were evolved. Then this primitive stock is conceived to have split into two lines, one of which continued its evolution along the same lines as the parent stock. The other line (araucarians) faced about and began the reacquisition of the characters that had been lost. It almost completely regained the original type of pitting, lost all trace of its pitted rays, and almost totally lost the ability to produce resin canals in the wood. The history of other characters is much the same. The adherents of this theory do not seek to deny these resemblances nor the necessity of showing that they have been secondarily acquired. I have already set forth the evidence through which they believe that they have proved this astounding evolutionary sequence. So far as resemblance or likeness goes, the cordaitean theory is far and away the more probable.

On the basis of fossil history there is not much to choose in respect to antiquity of the two families, though the Araucarineae have, perhaps, at present the more certain record in the older rocks. Still, specialized abietineans are known so far back that we must assume their origin to have been very much farther back. I shall speak of the bearing of the transitional fossils of the Mesozoic after discussing the remaining canons of evidence, because it is only in the light of the inferences made in accord with them that these fossils can be made to support this theory. On the basis of geological sequence they favor the cordaitean theory, inasmuch as the older forms are more araucarian and the more recent ones more like modern Pinaceae, particularly certain Taxodineae and Sequoiineae.

Though the argument from resemblance and geological sequence is unfavorable to this theory, there are, nevertheless, a great many known facts that can be best explained in accordance with it. The evidence derived from a study of vestigial structures, recapitulations, traumatic reversions, and monstrosities largely favors this theory, though many facts are known which appear to be inconsistent with it.

The pitting of the tracheids in the ovulate cones has been interpreted by THOMSON and JEFFREY in exactly opposite ways. The former calls attention to the multiseriate (3–5 rows) cordaitean pits of the older wood, and the latter to the uniseriate wood of the first few tracheids. To make matters worse, the former calls attention to araucarian pitting in abietinean cones and roots. This could, of course, be explained as a heritage from the cordaiteans.

The argument from recapitulation is hardly more fortunate. The seedling pine lacks spur shoots, just as does *Araucaria*, and hence spur shoots are not ancestral; but on the other hand the seedling *Araucaria* has abietinean pitting in the earlier annual rings.

Similarly, wounding an araucarian produces no resin canals, though it should if this theory be true; though wounding *Brachyphyllum* did. In other cases it does recall or induce abietinean characters.

The use that has been made of the bars of Sanio appears to the reviewer to fall in a class by itself. From the time of LINNAEUS' classification of flowering plants down to the present many such artificial distinctions have been proposed. They have usually been short-lived. Inasmuch as a bar of Sanio must have been at some time acquired, one would suppose that if you traced the ancestral line backward it would gradually fade out. In that case there would certainly be Abietineae somewhere along the line that lacked this structure. THOMPSON's discovery of its presence in mature secondary wood of modern araucarians renders its use of very doubtful value. It seems very unlikely that its mere absence from a mesozoic form otherwise unlike an araucarian is a character of sufficient importance to justify its inclusion in the Araucarineae.

The argument from abnormalities as applied to this theory is subject to attack on the historical side as well as on the ground of inherent probability. That a given abnormality represents always a reversion is an assumption that no one seriously maintains. For example, six toes are not uncommon in mankind. No one believes that this is an ancestral character any more than brachydactyly, where there are fewer parts than usual. An extra digit in hoofed animals is, on the contrary, usually looked on as a reappearance of an ancestral condition, because this condition is believed on other and trustworthy grounds actually to have occurred in this evolutionary line. In respect to the known conditions of the cones that may be supposed to be ancestral to modern pines, there is not a scintilla of evidence that they were any nearer the brachyblastic condition than their modern representatives. As I have already pointed out, the case is still more difficult in regard to the Cordaitales, the supposed remote ancestors, where the condition should, theoretically, be well developed. The strength of this theory is that it explains the pine cone, and its weakness is that it makes it necessary to apply the same explanation to other cones and shoots where it is very much less satisfying.

To sum up, the argument for the abietinean theory, therefore, is seen to be of a less convincing kind. Moreover, there are other arguments of the same kind that favor the cordaitean theory.

It seems clear to the writer, also, that there are well defined rules of evidence in the investigation of phylogenetic problems, but that the conclusions attained through their application have far less certainty than a chemical analysis or a mathematical prediction of a comet's course. With care the latter attains a high degree of certainty. The degree of probability in phylogenetic inquiries is more nearly that pertaining to the verdict of juries in our law courts. They are both always subject to attack by the introduction of new evidence.

Summary

1. The science of phylogeny possesses fairly adequate and reasonably trustworthy rules of evidence.

2. The degree of relationship is most clearly indicated by a detailed and accurate comparison of all the structures of the plant in all the stages of development, and is roughly proportional to the number and exactness of the resemblances.

3. Conclusions derived from direct comparisons should be checked carefully by the geological record.

4. Direct comparisons may be supplemented by indirect comparisons instituted through the use of more or less valid conclusions derived from the presence of supposed vestigial structures in primitive regions and from recapitulationary phenomena. Such indirect comparisons afford much less certain conclusions.

5. Reversions to ancestral conditions may sometimes occur under normal conditions or be experimentally produced by wounding or unusual conditions of growth. Conclusions based on evidence of this sort have little weight unless supported by other more reliable sorts of evidence.

6. Gymnosperms as a group resemble one another much more closely in very many ways than any one of them resembles any other group. They are, therefore, monophyletic. Since the cycadophytes are almost certainly derived from a filicinean ancestry, it follows that all are ultimately traceable to the same source.

7. The conifers closely resemble Cordaitales and are probably derived from them.

8. Araucarineae resemble the Cordaitales far more closely than do any other conifers, and are probably derived directly from them. This conclusion is consistent with the geological record.

9. The transitional conifers of the Mesozoic are either araucarians or cordaiteans well on their way toward Pinaceae. Some of them may be actually ancestral to such Taxodineae as *Cryptomeria* and *Sequoia*.

10. The Abietineae are very old and are derived either directly from the Cordaitales or from the very ancient members of the Araucarineae.

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LITERATURE CITED

1. BAILEY, IRVING W., The structure of the wood in the Pineae. BOT. GAZ. **48**:47–55. *pl. 5.* 1909.
2. ———, A cretaceous *Pityoxylon* with marginal tracheids. Ann. Botany **25**:315–325. 1911.
3. BENSON, MARGARET, *Miadesmia membranacea* Bertrand; a new paleozoic lycopod with seedlike structure. Phil. Trans. Roy. Soc. London B **199**: 409–425. *pls. 33–37.* 1908.
4. BURLINGAME, L. L., The staminate cone and male gametophyte of *Podocarpus*. BOT. GAZ. **46**:161–178. *pls. 8, 9.* 1908.
5. ———, The morphology of *Araucaria brasiliensis*. I. The staminate cone and male gametophyte. BOT. GAZ. **55**:97–114. *pls. 4, 5.* 1913.
6. ———, *idem.* II. The ovulate cone and female gametophyte. BOT. GAZ. **57**:490–508. *pls. 25–27.* 1914.
7. ———, *idem.* III. Fertilization, the embryo, and the seed. BOT. GAZ. **59**:1–39. *pls. 1–3.* 1915.
8. CAMPBELL, D. H., Mosses and ferns. New York. 1905.
9. ———, Plant life and evolution. New York. 1911.
10. CHRYSLER, M. A. (with JEFFREY), The microgametophyte of the Podocarpineae. Amer. Nat. **41**:355–364. 1907.
11. ———, (with JEFFREY), On Cretaceous Pityoxyla. BOT. GAZ. **42**:1–15. *pls. 1, 2.* 1906.
12. ———, Tyloses in tracheids of conifers. New Phytol. **7**:198–294. *pl. 5.* 1908.
13. ———, The origin of the erect cells in the phloem of the Abietineae. BOT. GAZ. **56**:36–50. 1913.
14. COULTER, JOHN M., Recent advances in the study of vascular anatomy. Amer. Nat. **43**:219–230. 1909.
15. ———, Evolutionary tendencies among gymnosperms. BOT. GAZ. **48**: 81–97. 1909.
16. ——— (with CHAMBERLAIN), Morphology of gymnosperms. Chicago. 1910.
17. ———, History of gymnosperms. Pop. Sci. Monthly. February 1912.
18. ———, Phylogeny and taxonomy. Amer. Nat. **46**:215–225. 1912.
19. EAMES, ARTHUR J., The morphology of *Agathis australis*. Ann. Botany **27**:1–38. *pls. 1–4.* 1913.
20. GERRY, ELOISE, The distribution of the bars of Sanio in the Coniferales. Ann. Botany **24**:119–124. *pl. 13.* 1910.
21. GOTHAN, W., Über die Wandlungen der Hoftüpfelung bei den Gymnospermen, im Laufe der geologischen Epochen und ihre physiologische Bedeutung. Sitzungs. Gesells. Naturf. Freunde Berlin. no. 2. 1907.
22. ———, Die fossiler Holzresten von Spitsburgen. Kungl. Svensk. Vetensk. Handl. **45**: no. 8. 1910.

23. HOLDEN, RUTH, Ray tracheids in the Coniferales. BOT. GAZ. **55**:56–65. *pls. 1, 2.* 1913.
24. ———, Permian and triassic fossils from New Brunswick and Prince Edward Island. Ann. Botany **27**:243–255. 1913.
25. ———, Coniferous jurassic woods from Yorkshire. Ann. Botany **27**:535–545. 1913.
26. HUTCHINSON, A. H., The male gametophyte of *Abies*. BOT. GAZ. **57**:148–153. 1914.
27. JEFFREY, EDWARD C., The development, structure, and affinities of the genus *Equisetum*. Mem. Boston Soc. Nat. Hist. **5**:155–190. *pls. 26–30.* 1899.
28. ———, The morphology of the central cylinder in the angiosperms. Trans. Canad. Inst. **6**:1–40. *pls. 7–11.* 1900.
29. ———, The structure and development of the stem in Pteridophyta and Gymnosperms. Phil. Trans. Roy. Soc. London B **195**:119–146. *pls. 1–6.* 1902.
30. ———, The comparative anatomy and phylogeny of the Coniferales. I. The genus *Sequoia*. Mem. Boston Soc. Nat. Hist. **5**:441–459. *pls. 68–71.* 1903.
31. ———, *idem.* II. The Abietineae. Mem. Boston Soc. Nat. Hist. **6**:1–37. *pls. 1–7.* 1904.
32. ——— (with HOLLICK), Affinities of certain cretaceous plant remains commonly referred to the genera *Dammara* and *Brachyphyllum*. Amer. Nat. **40**:189–216. *pls. 1–5.* 1906.
33. ——— (with CHRYSLER), On cretaceous Pityoxyla. BOT. GAZ. **42**:1–15. *pls. 1, 2.* 1906.
34. ———, The wound reactions of *Brachyphyllum*. Ann. Botany **20**:383–394. *pls. 27, 28.* 1906.
35. ———, *Araucariopitys*, a new genus of araucarians. BOT. GAZ. **44**:435–444. *pls. 27–30.* 1907.
36. ——— (with CHRYSLER), The microgametophyte of the Podocarpineae. Amer. Nat. **41**:355–364. 1907.
37. ———, On the structure of the leaf in cretaceous pines. Ann. Botany **22**:207–220. *pls. 13, 14.* 1908.
38. ———, A new araucarian genus from the Triassic. Proc. Boston Soc. Nat. Hist. **34**:325–332. *pls. 31, 32.* 1910.
39. ———, A new *Prepinus* from Martha's Vineyard. Proc. Boston Soc. Nat. Hist. **34**:333–338. *pl. 33.* 1910.
40. ———, On the affinities of the genus *Yezonia*. Ann. Botany **32**:767–773. *pl. 65.* 1910.
41. ———, The affinities of *Geinitzia gracillima*. BOT. GAZ. **51**:21–27. *pl. 8.* 1911.
42. ———, The history, comparative anatomy, and evolution of the *Araucarioxylon* type. Proc. Amer. Acad. **48**:531–571. *pls. 1–8.* 1912.

43. LLOYD, FRANCIS E., Morphological instability, especially in *Pinus radiata*. BOT. GAZ. **57**:314–319. *pl. 14.* 1914.
44. NOREN, C. O., Zur Kenntniss der Entwicklung von *Saxegothaea conspicua*. Svensk. Bot. Tidsk. **2**:101–122. *pls. 7–9.* 1908.
45. OLIVER, F. W., On the origin of gymnosperms (at the Linnaean Society). New Phytol. **5**:68–70, 147. 1906.
46. PENHALLOW, D. P., North American species of *Dadoxylon*. Proc. Roy. Soc. Canada **6**:51–79. 1900.
47. POTONIÉ, H., Lehrbuch der Pflanzenpalaeontologie. Berlin. 1899.
48. RENAULT, B., Structure comparée de quelques tiges de la flore carbonifère. Nouv. Arch. Mus. II. **2**:213–348. *pl. 8.* 1879.
49. SCOTT, D. H., On *Spencerites*, a new genus of lycopodiaceous cone. Phil. Trans. Roy. Soc. B **189**:83–106. *pls. 12–15.* 1897.
50. ———, On *Cheirostrobus*, a new type of fossil cone from the Lower Carboniferous strata. Phil. Trans. Roy. Soc. B **189**:1–34. *pls. 1–6.* 1897.
51. ———, The seedlike fructification of *Lepidocarpon*. Phil. Trans. Roy. Soc. B **194**:291–333. *pls. 38–43.* 1901.
52. ———, On the origin of gymnosperms (at the Linnaean Society). New Phytol. **5**:141–145. 1906.
53. ———, Studies in fossil botany. London. 1909.
54. SEWARD, A. C., and FORD, SYBILLE, The Araucariae recent and extinct. Phil. Trans. Roy. Soc. B **198**:305–411. *pls. 23, 24.* 1905.
55. SEWARD, A. C., On the origin of gymnosperms (at the Linnaean Society). New Phytol. **5**:73–76. 1906.
56. SIFTON, H. B., Cycad pitting. Science N.S. **39**:261. 1914.
57. SINNOTT, EDMUND W., *Paracedroxylon*, a new type of araucarian wood. Rhodora **11**:165–173. *pls. 80, 81.* 1909.
58. ———, Some features of the anatomy of the foliar bundle. BOT. GAZ. **51**:258–271. *pl. 17.* 1911.
59. ———, The morphology of the reproductive structures in the Podocarpineae. Ann. Botany **27**:39–82. *pls. 5–8.* 1913.
60. STILES, WALTER, The anatomy of *Saxegothaea conspicua*. New Phytol. **7**:209–222. 1908.
61. ———, The Podocarpeae. Ann. Botany **26**:443–514. *pls. 46–48.* 1912.
62. STOPES, MARIE C. (with FUJII), Studies on the structure and affinities of cretaceous plants. Phil. Trans. Roy. Soc. B **201**:1–90. *pls. 1–9.* 1910.
63. ———, A reply to Professor JEFFREY'S article on *Yezonia* and *Cryptomeriopsis*. Ann. Botany **25**:269. 1911.
64. ———, A new *Araucarioxylon* from New Zealand. Ann. Botany **28**:341–350. *pl. 20.* 1914.
65. STRASBURGER, ED., Histologische Beiträge III. 1891.
66. THISTLETON-DYER, SIR W. T., Persistence of leaf traces in Araucarineae. Ann. Botany **15**:547–548. 1901.

67. THOMSON, ROBERT BOYD, On the origin of gymnosperms (at the Linnaean Society). New Phytol. **5**:144–145. 1906.
68. ———, On the pollen of *Microcachrys tetragona*. BOT. GAZ. **47**:27–29. *pls. 1–2.* 1909.
69. ———, The megasporophyll of *Saxegothaea* and *Microcachrys*. BOT. GAZ. **47**:345–354. *pls. 22–25.* 1909.
70. ———, On the comparative anatomy and affinities of the Araucarineae. Phil. Trans. Roy. Soc. B **204**:1–50. *pls. 1–7.* 1912.
71. ——— (with ALLIN), Do the Abietineae extend to the Carboniferous? BOT. GAZ. **53**:339–344. *pl. 26.* 1912.
72. ———, On the origin of the resin tissue of the conifers. Science N.S. **39**:261. 1914.
73. ———, The spur shoot of the pines. BOT. GAZ. **57**:362–384. *pls. 20–23.* 1914.
74. ———, Reviews of Miss HOLDEN's papers. BOT. GAZ. **57**:80–83. 1914.
75. THOMPSON, W. P., The origin of ray tracheids in the Coniferae. BOT. GAZ. **50**:101–116. 1910.
76. TISON, A., Sur le *Saxegothaea conspicua*. Caen. 1909.
77. WORSDELL, W. C., On the origin of gymnosperms (at the Linnaean Society). New Phytol. **5**:146–147. 1906.
78. ———, The structure of the female flower in Coniferae. Ann. Botany **14**:39–82. 1900.